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Quantifying the invasiveness of species

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Abstract

The success of invasive species has been explained by two contrasting but non-exclusive views: (i) intrinsic factors make some species inherently good invaders; (ii) species become invasive as a result of extrinsic ecological and genetic influences such as release from natural enemies, hybridization or other novel ecological and evolutionary interactions. These viewpoints are rarely distinguished but hinge on distinct mechanisms leading to different management scenarios. To improve tests of these hypotheses of invasion success we introduce a simple mathematical framework to quantify the invasiveness of species along two axes: (i) interspecific differences in performance among native and introduced species within a region, and (ii) intraspecific differences between populations of a species in its native and introduced ranges. Applying these equations to a sample dataset of occurrences of 1,416 plant species across Europe, Argentina, and South Africa, we found that many species are common in their native range but become rare following introduction; only a few introduced species become more common. Biogeographical factors limiting spread (e.g. biotic resistance, time of invasion) therefore appear more common than those promoting invasion (e.g. enemy release). Invasiveness, as measured by occurrence data, is better explained by inter-specific variation in invasion potential than biogeographical changes in performance. We discuss how applying these

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comparisons to more detailed performance data would improve hypothesis testing in invasion biology and potentially lead to more efficient management strategies.

Keywords
Biogeographical comparisons, biological invasions, preadaptation, functional traits, increased vigour, invasion success, intrinsic vs extrinsic factors

Introduction

The economic and ecosystem impacts caused by species invasions are considerable (Gaertner et al. 2009; Pyšek et al. 2012b). However, the vast majority of species that are introduced remain rare, with only a fraction becoming widespread and dominating local communities (Williamson and Fitter 1996; Jeschke and Strayer 2005; Ricciardi and Kipp 2008; Stohlgren et al. 2011; Hulme 2012). Identifying the ecological and evolutionary factors that determine these disparate outcomes is the focus of a large body of published empirical work (van Kleunen et al. 2010a) including a growing number of hypotheses and synthetic frameworks (Catford et al. 2009; Blackburn et al. 2011; Gurevitch et al. 2011; Jeschke et al. 2012).

One reason for this expanding literature is a growing appreciation for the inherent complexity of ecological and evolutionary (eco-evolutionary) processes. But an additional factor may be a lack of appropriate data to rigorously evaluate multiple hypotheses for invasion success and the circumstances under which they are most applicable. To further explore this latter possibility, we review the hypotheses suggesting that some plant species are inherently good invaders, and those suggesting that invasiveness is acquired as a result of ecological and genetic differences between the native and introduced range. We introduce two simple metrics for quantifying the invasiveness of species on a relative scale and demonstrate their utility using occurrence data of native and introduced plant species in Argentina, South Africa, and Europe. We demonstrate how inter- and intraspecific comparisons using field surveys can improve testing of the major hypotheses of invasion success, and identify a significant data gap – namely, the lack of comprehensive field data measuring survival and reproductive rates in natural populations.

Hypotheses of invasion success

Hypotheses proposed to explain invasion success can generally be grouped into two categories based on whether they primarily attribute invasion success or failure to (i) extrinsic differences in ecological or evolutionary processes that differ between native and introduced ranges or (ii) intrinsic biological characteristic of particular species or higher-order taxonomic groups. Two key assumptions underlie these hypotheses. First, if invasiveness arises as a result of eco-evolutionary differences between the native and introduced ranges, then introduced populations in the introduced range should

exhibit enhanced performance relative to their conspecifics in the native range. Alternatively, if invasiveness is primarily an inherent characteristic, then invasive species should perform well in both ranges.

Perhaps the most common hypotheses in contemporary studies are those attributing the successful proliferation and spread of invasive species to altered ecological and evolutionary processes, an idea which dates back to the foundational literature of biological invasions (Elton 1958; Baker and Stebbins 1965). For example, introduced species experience an inhospitable abiotic environment (Mack 2000), or biotic resistance due to competition (Levine et al. 2004) or damage by native enemies (Parker et al. 2006), limiting the establishment, spread, and impact of the majority of introduced species. Additionally, establishment may fail because of insufficient propagule pressure (Lockwood et al. 2005) and Allee effects (Allee 1931), leading to stochastic extinction (Sax and Brown 2000). Alternatively, species may overcome these barriers given sufficient time (Pyšek and Jarošík 2005; Williamson et al. 2009), or by virtue of novel allelochemicals (Callaway and Ridenour 2004), altered soil microbial interactions (Reinhart and Callaway 2006), novel mutualisms (Richardson et al. 2000), and loss of natural enemies during the invasion process (Mitchell and Power 2003; Torchin et al. 2003). Introduction of historically isolated populations or species could also result in novel opportunities for interspecific hybridization leading to hybrid vigour in the introduced range (Ellstrand and Schierenbeck 2000), or intraspecific hybridization among historically isolated populations could occur, leading to novel adaptive gene combinations or simply increasing standing genetic variation available for adaptive evolution (Kolbe et al. 2004; Keller and Taylor 2010). Additionally, invaders are likely to be successful if they fill a novel role or function within an invaded ecosystem (Fetahi et al. 2011), if they are able to use resources not completely used by natives (Case 1990), or if they interact in novel ways with other non-native species (Simberloff and Von Holle 1999). Regardless of the specific mechanisms proposed, all of the hypotheses mentioned above assume that ecological or genetic differences between the native and introduced ranges (i.e. extrinsic factors) are responsible for making species invasive.

An alternative class of hypotheses regard invasiveness as an intrinsic quality of some species, implicitly assuming that ecological differences between ranges are minor relative to the identity and functional traits of the invader. This idea also dates back to early literature on invasive species, particularly Baker's (1965) characterization of a hypothetical 'ideal weed' possessing a particular suite of traits associated with invasiveness. Baker also noted that some invasive species exhibit a 'general purpose genotype' with high phenotypic plasticity and fixed heterozygosity, which he hypothesized made them capable of occupying a broad range of habitats in their native and introduced ranges (Baker 1965). These ideas have stimulated a large number of studies suggesting particular traits that promote invasion, but few generalities have emerged (Pyšek and Richardson 2007; van Kleunen et al. 2010b). However, the traits of invasive species are often similar to abundant or widespread native species (Lind and Parker 2010; van Kleunen et al. 2010b), suggesting that it may be possible to predict performance based on species' traits alone. The use of key traits or trait combinations to predict a spe-

cies' potential invasiveness has obvious management benefits, including the creation of 'blacklists' of potentially harmful species, 'whitelists' of species unlikely to pose a significant threat (Kolar and Lodge 2002; Hui et al. 2011), and formal risk assessment for particular applications (Kumschick and Richardson 2013). Interestingly, if invasions are the result of traits intrinsic to the invader *per se*, some species may simply be ecologically dominant both home and away - a quantitative prediction that has received surprisingly little attention in the literature despite the profound impacts it would have on our understanding and management of invasions (Firn et al. 2011).

Inter- vs. intra-specific comparisons

The contrasting hypotheses outlined above attribute the successful (or failed) spread and proliferation of introduced species to either (i) intrinsic differences in performance among species (or higher-level taxonomic groups) often manifested through functional traits, or (ii) extrinsic consequences of the invasion process (e.g., release from natural enemies, novel weapons, biotic resistance). Two types of data would be particularly helpful to explore these alternatives. First, field data are needed to quantify the performance of introduced species relative to other species within a particular community or assemblage (i.e. interspecific field comparisons). Second, field data from populations of individual species are needed to compare biogeographical differences in performance between the native and introduced ranges (i.e. intraspecific field comparisons).

Inter- and intra-specific field comparisons can be conceptualized as separate but non-independent axes along which to classify invasiveness in a purely ecological context (Fig. 1). The interspecific comparison axis (ω) quantifies the ecological performance or 'invasiveness' of a species in its introduced range without regard to the mechanisms responsible. Here we define invasiveness as a composite measure of performance of introduced species, particularly rates of survival and reproduction in natural populations that lead to high abundance and competitive exclusion of native species. The intraspecific comparison axis (δ) quantifies the degree to which performance changes from the native to the introduced range resulting from differences in ecological and evolutionary processes. Note that performance measurements may include abundance, survival, reproduction, or more complex population demographic parameters.

Comparing species along the axes in Fig. 1 could provide a simple but powerful characterization of whether a particular species is invasive because it performs well everywhere ($\omega >> 0$ and $\delta \sim 0$ in Fig. 1), or because it benefits from eco-evolutionary differences between ranges ($\omega >> 0$ and $\delta > 0$). This comparison can also distinguish non-invasive species ($\omega << 0$) that are successful natives that fail to become invasive as a result of eco-evolutionary differences between ranges ($\delta < 0$), from species that are simply rare species regardless of range ($\delta \sim 0$). Moreover, the literature tends to inconsistently categorize species as 'invasive' if they have large economic or ecological impacts (Daehler 2001, Richardson et al. 2011), treating invasive and non-invasive species as distinct categories, whereas our approach quantifies invasiveness along a continuum.

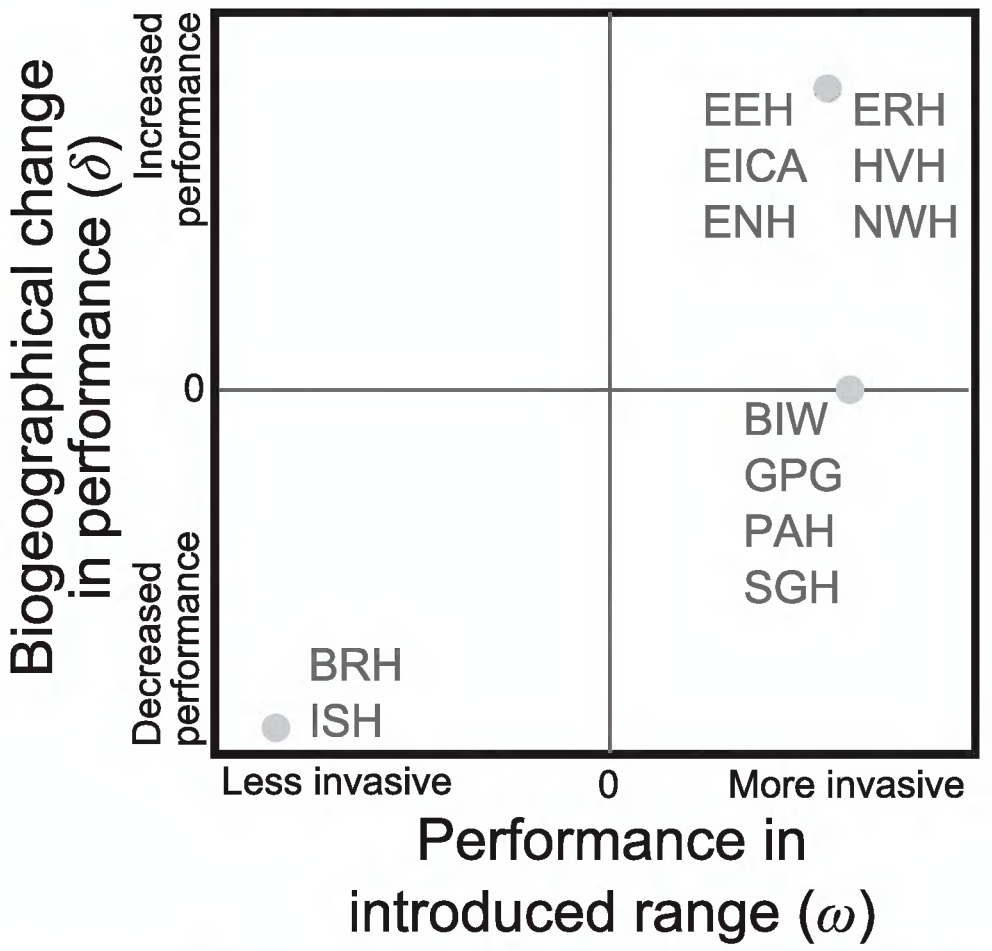

Figure 1. Testing hypotheses of invasion success could be improved by quantifying interspecific (ω) variation in performance among introduced species and intraspecific (δ) changes in performance between introduced and native populations. Dots show relative positions of a species predicted by the enemy of my enemy hypothesis (EEH), evolution of increased competitive ability (EICA), empty niche hypothesis (ENH), enemy release hypothesis (ERH), hybrid vigour hypothesis (HVH), novel weapons hypothesis (NWH), Baker's ideal weed (BIW), general purpose genotype (GPG), pre-adaptation hypothesis (PAH), specialist-generalist hypothesis (SGH), biotic resistance hypothesis (BRH), and the increased susceptibility hypothesis (ISH).

Quantifying the invasiveness of species could motivate appropriate study organisms for testing particular hypotheses of invasion success. For example, the enemy release hypothesis predicts that invasiveness results from native-introduced differences in the communities of natural enemies (Keane and Crawley 2002), which should yield an increase in performance ($\delta > 0$). Similarly, species that do not benefit from escaping natural enemies should have similar performance in the native and introduced ranges ($\delta \sim 0$), whereas those that gain more harmful enemies should have reduced performance in the introduced range ($\delta < 0$), on average. A more quantitative prediction of the enemy release hypothesis is therefore a positive relationship between the degree of escape from natural enemies and δ. Analogous predictions from other hypotheses of invasion success are approximated in Fig. 1.

In addition to simple statistical correlations, incorporating field measurements of ω and δ as continuous variables can lead to more rigorous statistical tests of invasion success. For example, simple least-squares models or more advanced statistical approaches, such as a path analysis (Wootton 1994), might be used to test one or more predictor variables on ω and δ, such as the degree of escape from natural enemies, or changes in allelopathic chemicals, or extent of genetic admixture. Other factors could

be incorporated in such an analysis to control for time of invasion, phylogenetic relatedness or to test the relative importance of different hypotheses. Importantly, a path analysis could test direct effects on invasiveness (ω), indirect effects on invasiveness via biogeographical differences in performance (δ), and the relative effect to ω and δ of the different predictor variables examined. Below we present a general mathematical approach to quantify inter- and intraspecific field measurements of performance, and then we demonstrate their heuristic and analytical value using occurrence data for plant species in Argentina, South Africa, and Europe.

Quantifying inter- vs. intra-specific difference in performance

A simple index that compares the relative performance (*W*) of a focal species (*j*) in a pool of *S* species is the following log ratio:

(Eq. 1) $$\omega_j = ln\left(S * W_j / \sum_{x=1}^{S} W_x\right)$$

This equation is simply performance (*W*) measured for a focal species (*j*) divided by the average performance of all species (*S*) in the pool. It is designed to quantify interspecific variation in performance on a relative scale, which is necessary to compare the same species in different habitats or in different species assemblages. For example, performance could be measured as the relative abundance of an introduced species and compared across habitats with different species communities and productivity levels (e.g. Firn et al. 2011).

Quantifying performance on a relative scale provides a convenient method for comparing a species in its native and introduced ranges. For example, to quantify the biogeographical change in performance of an introduced species, consider the log-ratio of the relative performance of species *j* (from Eq. 1) calculated in its native (*n*) and introduced (*i*) ranges (see also Hufbauer and Torchin 2007), or:

$$\delta_j = ln\left(\frac{S_i * W_{j,i} / \sum_{x=1}^{S_i} W_{x,i}}{S_n * W_{j,n} / \sum_{y=1}^{S_n} W_{y,n}}\right)$$

which is mathematically equivalent to the difference in Eq. 1 between the native (ω_n) and introduced (ω_i) ranges:

(Eq. 2) $$\delta = \omega_i - \omega_n$$

Using the intraspecific comparison given by Eq. 2, a positive δ represents an increase in the relative performance of species in the introduced range compared to the native range ($\omega_i > \omega_n$), whereas a negative value represents a decrease in relative performance ($\omega_i < \omega_n$).

One potential limitation of having non-independent axes is that an error in calculating ω_i will also increase δ_i, leading to spurious correlations if the same performance data are used. One solution to this problem would be to calculate these indices from different performance measurements. For example, one could calculate ω_i using range size, but measure intrinsic growth rates of native and introduced field populations to calculate δ_i. Incorporating these into the kind of statistical framework described above would be useful to test whether an extrinsic factor of interest (e.g. enemy release, heterosis) could explain differences in population vital rates between native and introduced populations (δ) and whether this could account for variation in range size (ω), after controlling for other factors like time since invasion and phylogenetic relatedness. The choice of performance measurements used to calculate ω and δ will ultimately depend on the hypotheses to be addressed.

In addition to testing scientific hypotheses, this approach could help to guide management decisions. For example, species found in the top left quadrant of Fig. 1 have increased performance in the introduced range, perhaps by escaping enemies or otherwise experiencing novel conditions, but have not (yet) become invasive. These species may become invasive if ecological conditions change (e.g., habitat alteration, global warming) or just given enough time (e.g., finding suitable habitats, evolutionary adaptation). These species may provide a high return on investment in control programs as they represent introduced species that are likely to become more invasive if proper measures are not taken. Additionally, species in the lower left quadrant are introduced species that are currently not invasive but could be if ecological conditions become more similar to those in the native range, for example with new disturbance regimes or a changing climate. Identifying several of these potential invaders within a particular region or habitat might help to motivate conservation efforts to limit anthropogenic influences that would cause these species to become more invasive.

Despite the scientific and management value of this approach, even simple performance measurements such as annual survival and reproductive rates are not available for most species in most regions. Given this limitation, we instead apply occurrence data available from plant species surveys to demonstrate the potential utility of Eqs. 1 and 2.

Example: occurrence data

To demonstrate the value of the inter- and intra-specific comparisons described above, we analysed occurrence data that has previously been published (Stohlgren et al. 2011). These data are simply the occupancy rates of individual plant species in 10 × 10 km cells in Great Britain (Preston et al. 2002), 11 × 12 km cells in the Czech Republic (from the CzechFlor database), 0.25-degree cells in the Republic of South Africa (Henderson 1998; Germishuizen and Meyer 2003), across 23 countries in Europe (Winter et al. 2008; DAISIE 2009), and 24 bioregional sub-regions in Argentina (Zuloaga and Morrone 1996). In other words, each regional dataset includes an inventory list of all native and introduced species identified in each region, as well as the number of cells (or countries or bioregions) in which each species is known to occur.

Importantly these data are not sufficient to account for potential influence of phylogenetic non-independence and time of invasion. Residence time in particular can have a large impact on spread measured at a particular point in time (Pyšek and Jarošík 2005; Williamson et al. 2009). Moreover, species occurrence data represent only a rough approximation of numerical abundance and dominance (Royle and Dorazio 2008). Occurrence data will tend to over-estimate the invasiveness of species that are weak competitors but widespread, while under-estimating the invasiveness of recently established species that dominate where present but are not yet widely distributed. Our analysis is therefore intended as an introduction to the utility of the metrics described above, rather than to provide a definitive quantification of invasiveness.

We used Eq. 1 to quantify the performance of each species (ω_i) within each regional dataset as the number of occupied geographic cells relative to the number of cells averaged across all native and introduced species in a given region. The relative performance index of each species (ω_i) in its native and introduced ranges is shown in Fig. 2 for each of the eight pairwise comparisons between regional datasets. We include both pairwise transcontinental comparisons (Europe, Argentina and South Africa) and a within-continent contrast between the Czech Republic and Britain. This demonstrates the utility of Eq. 1 to compare performance between regions despite differences in species communities and census cell sizes (e.g. 23 countries in Europe vs. 0.25 degree cells in South Africa).

We found that in each region the majority of introduced species (66.6%) rated below-average on the relative performance axis (ω) in the introduced range (Fig. 2, y-axis < 0; $G = 112.3$, 1 *d. f.*, $P < 0.001$). This includes recent invaders that are still spreading, but also is consistent with the generally accepted view that only a minority of introduced species are able to establish and spread widely (Williamson and Fitter 1996; Jeschke and Strayer 2005; Ricciardi and Kipp 2008; Stohlgren et al. 2011; Hulme 2012). The majority of introduced species may simply be intrinsically weak invaders, or extrinsic environmental factors such as biotic resistance, genetic bottlenecks or simply time since introduction could prevent them from becoming invasive. We found that most species (73.7%) experienced a reduction in relative performance compared to the native range (i.e. below 1:1 line in Fig. 2; $G = 233.9$, 1 *d. f.*, $P < 0.001$), suggesting that time since invasion and environmental, rather than intrinsic factors, often prevent species from becoming more common than they are in their native range.

After calculating relative performance of species between each pair of regional datasets, we used Eq. 2 to calculate biogeographical changes in relative performance of each species (Fig. 3). This equation simply uses the x and y coordinates of each species in Fig. 2 to calculate delta values (δ) for each introduced species in each region. The distribution of δ can provide insight into environmental and biotic differences between ranges given that $\delta_i = 0$ represents a species performing similarly in the native and introduced range. For example, the majority of species introduced from Argentina to Europe have decreased in relative performance ($\delta < 0$ in Fig. 3: AR-->EU), but species introduced from Argentina to South Africa have increased in relative performance, on average ($\delta < 0$ in Fig. 3: AR-->ZA). A number of factors could be investigated to explain the weaker

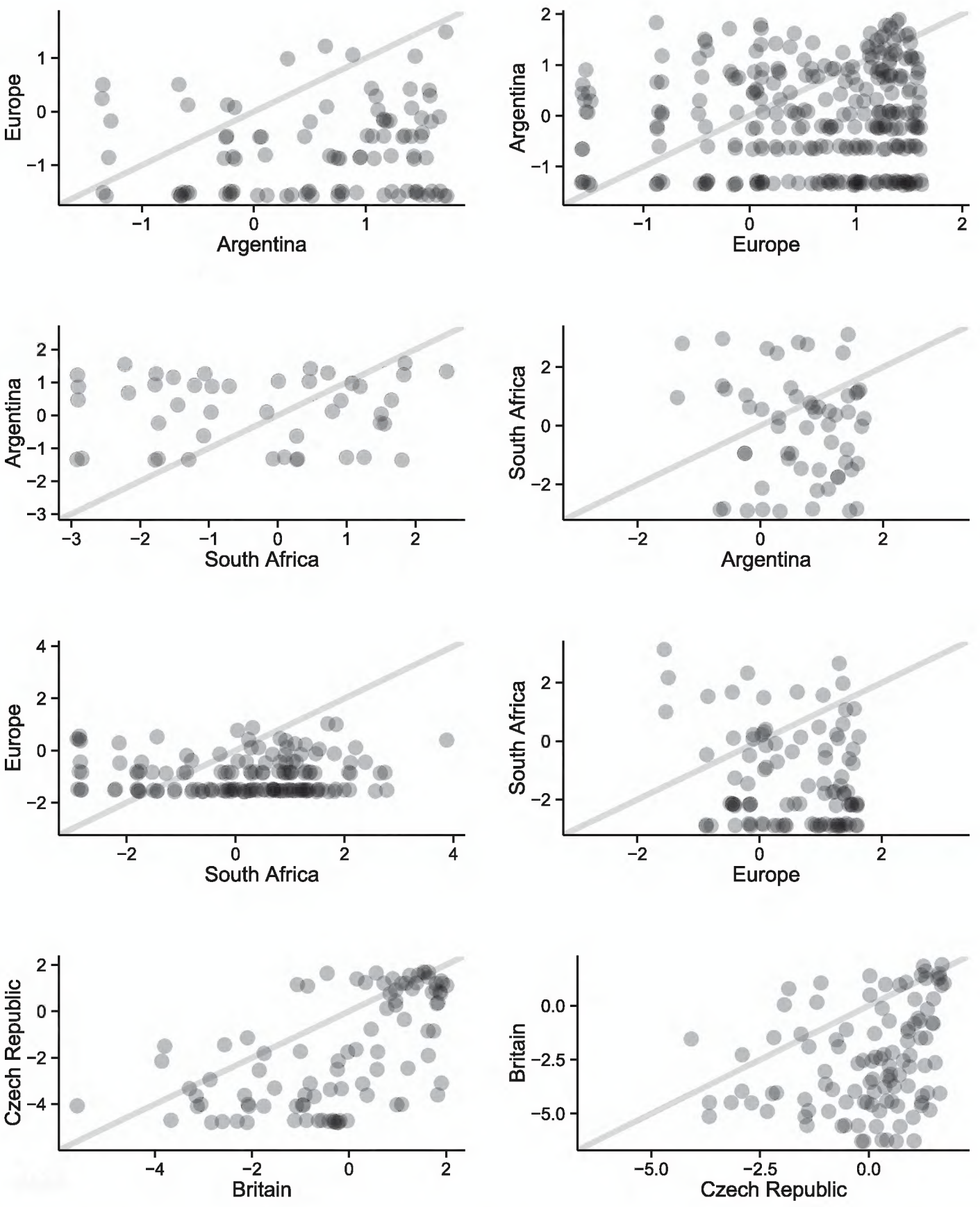

Figure 2. Bivariate plots comparing standardized performance measurements of species in their native (x-axis) and introduced ranges (y-axis). Each point is a species and the 1:1 line is shown in grey. Performance is measured as the number of occurrences, standardized for each region using Eq. 1 (see main text). Slight random noise was added to increase visibility of overlapping points.

performance of Argentinian native species in Europe relative to South Africa, such as stronger competition, or more aggressive generalist herbivores and diseases. Climate matching is also likely to be important given the reduced performance of European species introduced to South Africa (EU-->ZA) and Argentina (EU-->AR).

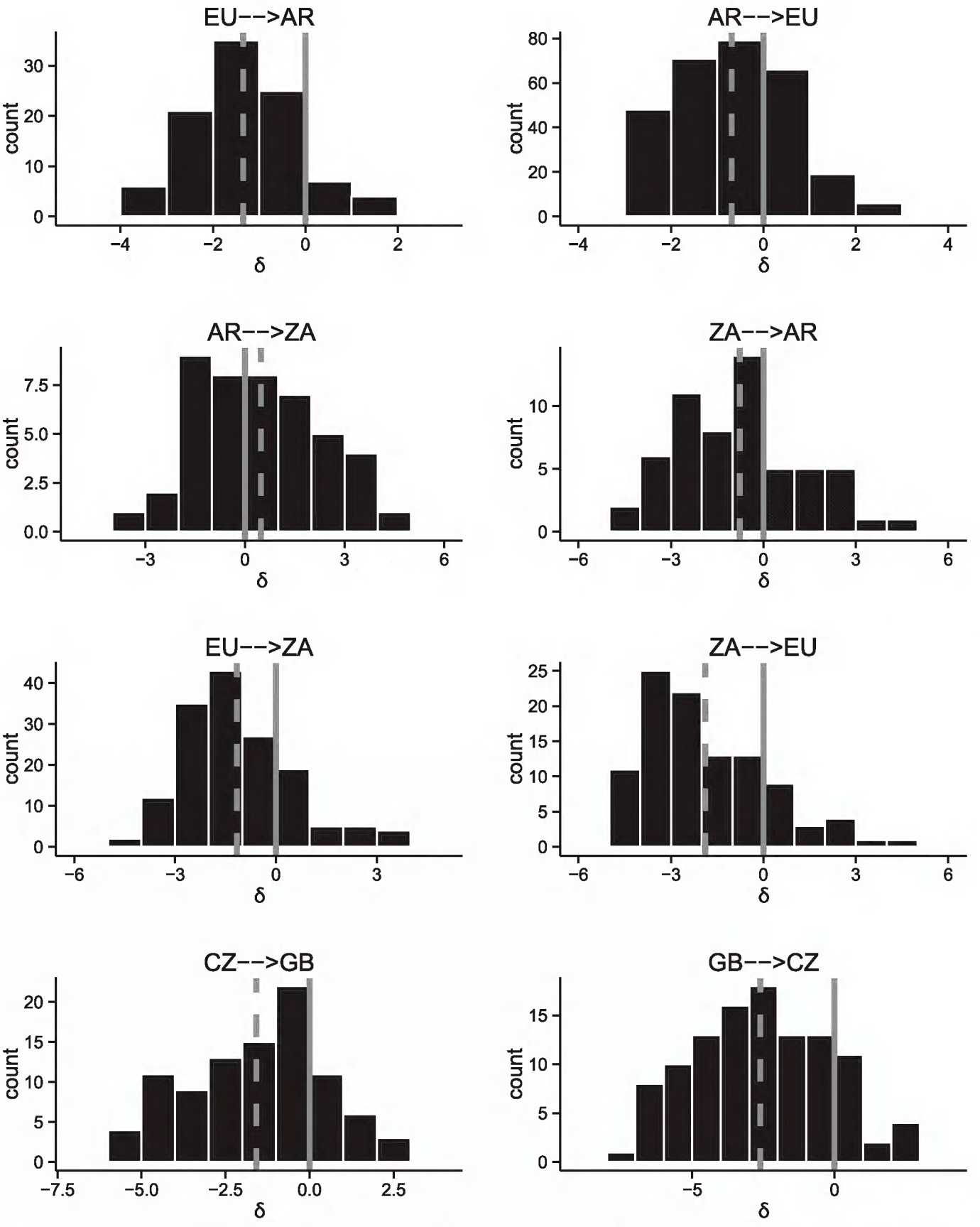

Figure 3. Frequency distribution histograms of biogeographical changes in performance (δ), for species native to one region and introduced to another, in the form of labels: "*native --> introduced*". Performance changes are based on the number of grid cells or regions of occurrence, standardized using Eq. 2 (see main text). Regions are abbreviated for Europe (EU), Argentina (AR), South Africa (ZA), the Czech Republic (CZ) and Britain (GB). Solid grey lines indicate equal performance in the native and introduced range, and the dotted lines shows the average δ.

Extrinsic ecological and genetic differences between the native and introduced range therefore appear to suppress most species from becoming common. But are the most common invaders more likely to belong to a subset of species that are common

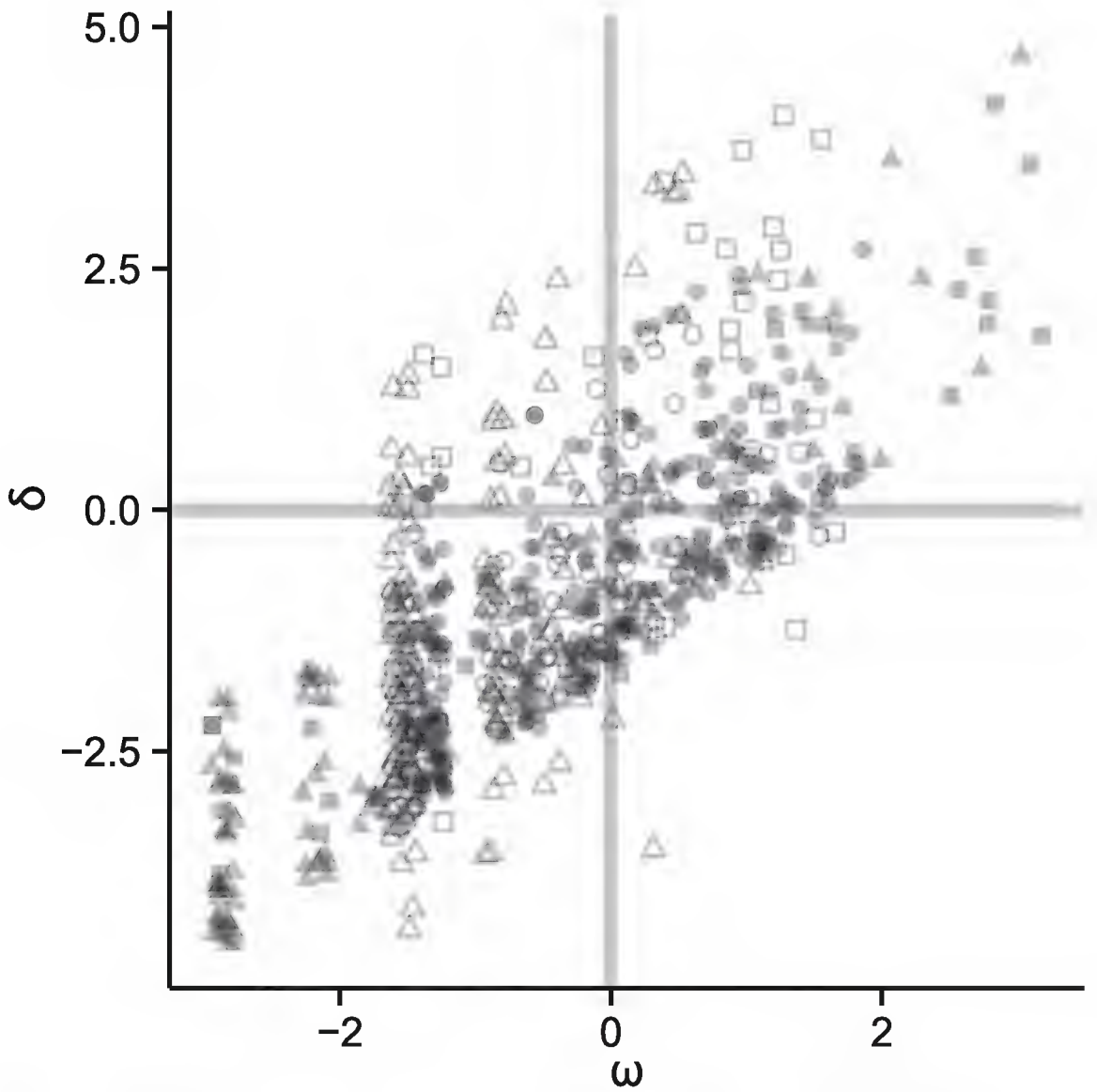

Figure 4. Bivariate plot of interspecific (x-axis) and intraspecific (y-axis) performance comparisons, using occurrence data. The x-axis shows performance of a species (ω) relative to the average performance of all species in its introduced range (ω = 0, vertical grey line). The y-axis shows the degree to which the biogeographical difference in performance (δ) deviates from equality in the introduced range relative to the native range (δ = 0, vertical grey line). Each point is an individual species from one of the following regional comparisons: species native to Europe and introduced to Argentina (open circles), Argentina to Europe (filled circles), Europe to South Africa (open triangles), South Africa to Europe (filled triangles), Argentina to South Africa (open squares), and South Africa to Argentina (filled squares). Slight random noise was added to increase visibility of overlapping points.

in their native range, or are they species that benefit most from eco-evolutionary processes (e.g. enemy release, novel weapons)? Following the heuristic approach in Fig. 1, we plotted ω and δ for each species in each pairwise comparison (Fig. 4) and found evidence for both scenarios. Of the 70 most common invaders ($\omega > 1.17$), 85% (60 of 70) increased their performance relative to the native range ($\delta > 0$), suggesting that extrinsic factors (e.g. enemy release, novel weapons, etc.) are important for explaining successful spread of the most common invaders. However, at any given point along the δ-axis in Fig. 4, species varied by up to an order of magnitude in ω, even though there is a strong correlation between these non-independent indices ($R = 0.866$). In other words, the extent of invasive spread (ω) varies significantly among species even after accounting for extrinsic environmental factors that cause differences in δ. Thus,

we find evidence that both intrinsic and extrinsic factors contribute to the relative invasiveness of species.

Simultaneously accounting for variability in both axes in Fig. 4 would improve statistical tests of invasion success, as measured by occurrence data. In particular, few characteristics of species successfully predict invasion success across a range of taxa (Pyšek and Richardson 2007; van Kleunen et al. 2010b). Without controlling for variation in δ, inherently good invaders are confounded with inherently poor invaders that become widespread due to extrinsic factors like enemy release or novel weapons. Similarly, inherently poor invaders are confounded with inherently good invaders that are prevented from becoming common by extrinsic factors like propagule pressure, a recent invasion history, or mismatched climate. In these cases, including δ in statistical tests for traits associated with ω would improve power to detect functional traits associated with inherently strong invaders.

In addition to examining intrinsic differences in invasion potential among species, extrinsic factors can also be better tested by accounting for variation in both axes in Fig. 4. Without accounting for variation in ω, introduced species that become common through extrinsic factors that increase performance are confounded with species that become common because they are inherently good invaders. Additionally, species that fail to become common because of reduced performance are confounded with species that are inherently poor invaders. Accounting for variation in ω would therefore improve statistical power to test for extrinsic genetic or environmental factors that influence the invasiveness of species. Testing enemy release, novel weapons, hybrid vigour, and other hypotheses for invasion success (or failure) based on extrinsic factors could be improved in this manner.

Despite the inherent limits of focusing our analysis on occurrence data, we have demonstrated above the potential value of using Eqs. 1 and 2 to better inform management decisions and to improve hypothesis testing. In the next section we consider alternative data sources for characterizing ω and δ that would significantly improve the approach we have advocated.

Improved performance measurements

Interspecific field comparisons

What sorts of data are available to quantify the performance of invasive species relative to other species within a particular community or assemblage? A number of studies have used an interspecific comparative approach to test hypotheses of invasion success. Many of these have been included in a recent meta-analysis (van Kleunen et al. 2010b), which reviewed data from 116 comparative studies involving 321 species. However, most of these (96%) did not distinguish invasive from non-invasive introduced species, but rather compared native and non-native species. In addition to the five remaining studies in the meta-analysis, we identified 27 studies that contrasted phenotypic traits or ecological aspects (e.g. herbivore load) of invasive and non-invasive introduced spe-

cies, several of which were published after the (van Kleunen et al. 2010b) meta-analysis (Table 1). We did not collect these studies using a methodical review of the literature but rather biased our search toward more recent studies demonstrating the different types of data currently available to quantify invasiveness for a large number of species (Table 1). Of these 32 studies, only four quantified invasiveness (Mihulka et al. 2003; Mitchell and Power 2003; Hamilton et al. 2005; Parker et al. 2006). The remaining 28 studies binned introduced species into two (24 of 28 studies) or more (4 studies in Table 1) categories of invasiveness.

These results show that comparative studies testing hypotheses of invasion success generally have used a categorical rather than a quantitative approach like the one we advocate in Figs 1–4. Moreover, invasiveness categories were determined primarily on expert opinion or presence/absence data in these studies, although occurrence data were occasionally combined with information on date of introduction to estimate rates of spread. This limited review therefore suggests that invasion biologists currently define species' invasiveness on a categorical scale, despite the obvious interspecific variation in performance that we demonstrate in Figs 2 and 4.

Intraspecific field comparisons

In addition to interspecific comparisons, testing hypotheses of invasion success also requires performance comparisons of natural field populations in the native and introduced range, yet these data are surprisingly rare (Firn et al. 2011). For example, a recent meta-analysis (Parker et al. 2013) compared size, reproductive traits, and abundance between native and introduced populations of the World's Worst Invaders (Lowe et al.

Table 1. Overview of interspecific comparative studies testing hypotheses of invasion success. The number of categories in a study is in parentheses for those using categorical classification. N is the number of species included in the study.

Citation	Invasiveness criteria	Classification	N
Burns 2004	Expert opinion	Categorical (2)	6
Burns and Winn 2006	Expert opinion	Categorical (2)	8
Cadotte et al. 2006	Occurrence data	Categorical (5)	1153
Cappuccino and Arnason 2006	Expert opinion	Categorical (2)	39
Cappuccino and Carpenter 2005	Expert opinion	Categorical (2)	18
Forcella et al. 1986	Expert opinion	Categorical (2)	3
Gerlach and Rice 2003	Expert opinion	Categorical (2)	3
Gioria et al. 2012	Occurrence and spread	Categorical (2)	321
Grotkopp and Rejmánek 2007	Spread rate	Categorical (2)	26
Hamilton et al. 2005	Occurrence data	Quantitative	152
Hejda et al. 2009	Occurrence and spread	Categorical (2)	282
van Kleunen et al. 2011	Occurrence data	Categorical (2)	28
Kubešová et al. 2010	Occurrence and spread	Categorical (2)	93

Citation	Invasiveness criteria	Classification	N
Lake and Leishman 2004	Expert opinion	Categorical (2)	57
Lloret et al. 2005	Expert opinion	Categorical (4)	354
Mihulka et al. 2003	Occurrence and spread	Quantitative	15
Mitchell and Power 2003	Expert opinion	Quantitative	473
Moravcová et al. 2010	Occurrence and spread	Categorical (2)	93
Murray and Phillips 2010	Expert opinion	Categorical (2)	468
Muth and Pigliucci 2006	Occurrence data	Categorical (2)	8
Nilsen and Muller 1980	Occurrence data	Categorical (2)	2
Parker et al. 2006	Expert opinion	Quantitative	51
Perrins et al. 1993	Spread rate	Categorical (4)	4
Phillips et al. 2010	Expert opinion	Categorical (2)	468
Pyšek and Jarošík 2005	Occurrence data	Categorical (3)	203
Pyšek et al. 2009a	Occurrence data	Categorical (2)	1218
Pyšek et al. 2009b	Occurrence and spread	Categorical (2)	17
Pyšek et al. 2011a	Occurrence and spread	Categorical (2)	1221
Pyšek et al. 2011b	Occurrence and spread	Categorical (2)	1007
Rejmánek and Richardson 1996	Spread rate	Categorical (2)	24
Richardson et al. 1987	Occurrence data	Categorical (2)	4
Skálová et al. 2011	Occurrence and spread	Categorical (2)	3

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2004). Despite an exhaustive search of the peer-reviewed and grey literature, performance data were not available for a majority of the investigated species (53 of 89), primarily because of a lack of published studies from the native range (Parker et al. 2013).

This paucity of performance data is surprising for plant taxa given the availability of large databases of presence/absence data (Zuloaga and Morrone 1996; Henderson 1998; Preston et al. 2002; Pyšek et al. 2002, 2012a; Germishuizen and Meyer 2003; Winter et al. 2008; DAISIE 2009; Stohlgren et al. 2011), and given that invasion biologists have repeatedly called for more studies from the native ranges of introduced species (Hierro et al. 2005; van Kleunen et al. 2010a). Impediments to progress on this front may include funding priorities, which tend to focus on problematic invaders and endangered native species. Increasingly the solution to data gaps might require the formation of international research networks and citizen-science efforts such as the "Nutrient Network" (http://nutnet.umn.edu), which is monitoring performance of hundreds of native and introduced plant species across 39 sites with similar habitat characteristics (Firn et al. 2011), or the "Global Garlic Mustard Field Survey" (http://www.garlicmustard.org), which measured performance of a single plant (*Alliaria petiolata*) across almost 400 sites in both its introduced and native ranges (Colautti et al 2014). More efforts like these could provide invaluable performance information to complement available distribution data for a variety of species.

In addition to these data limitations, it is often not clear which performance data are most appropriate for biogeographical comparisons. For example, one of the most common intraspecific comparison of invader performance is individual size (e.g. length or biomass), and sometimes time to maturity, ostensibly because fast-growing or long-lived individuals can become large and lead to increased population growth rates, population density, and abundance (Grime 1977). Individuals in introduced populations can indeed be larger in some species (Crawley 1987; Jakobs et al. 2004; Darling et al. 2011; Hinz et al. 2012, Parker et al. 2013), but other studies do not show a general increase in size between the native and introduced ranges (Thébaud and Simberloff 2001; Grosholz and Ruiz 2003). Moreover, many introduced plants form latitudinal clines in size and reproductive timing, suggesting that these traits are under divergent natural selection across large spatial scales (Colautti et al. 2009). Recent work on the invasive plant *Lythrum salicaria*, for example, shows that clines in size and reproductive timing arise because these traits trade off, resulting in an optimum phenotype that changes with latitude (Colautti and Barrett 2010; Colautti et al. 2010). Therefore, size and time to maturity in field populations may be poor measurements for contrasting native and introduced differences in performance. Population abundance and individual reproductive rates may be more informative performance metrics, but these have rarely been sampled in native and introduced populations even though these measurements are not difficult to obtain, particularly for plants (Vilà et al. 2005; Pergl et al. 2006; Ebeling et al. 2008). Measuring abundance, survival rates, and reproductive output of introduced species across their native and introduced ranges should be a priority for the field of invasion biology, as it would allow a quantitative comparison of different performance measures for assessing invasiveness.

Rates of survival and reproduction, as well as abundance data from natural field populations would be valuable for testing hypotheses of invasion success and setting management priorities. More to the point, the ideal dataset for testing the hypotheses of invasion success would include: (i) a census of all major life stages, and (ii) vital rates (i.e. survival and reproduction) at each life stage, perhaps with experimental manipulations and demographic modelling to better understand ecological dynamics of native and introduced populations (Williams et al. 2010; Roy et al. 2011). Additionally, time since invasion can be an important confounding factor if these vital rates change over time, increasing as introduced populations become locally adapted (Colautti et al. 2010) or decreasing as populations approach their carrying capacity (Lankau et al. 2009) and accumulate natural enemies (Hawkes 2007). Therefore, temporal replication of these measurements would also facilitate better models of invasive spread.

We recognize that although ideal, extensive spatial and temporal replication of demographic data and manipulative field experiments would be difficult to obtain for even a single species, let alone the dozens or hundreds needed to test the generality of invasion success hypotheses. We therefore wish to stress that even basic performance data would be a significant improvement over most currently available data. Given likely financial and time constraints, large-scale sampling efforts that quantify relatively simple performance measurements in a large number of populations across entire native and introduced distributions should be a priority. Measurements of abundance, survival and reproductive rates as a complement to large presence-absence datasets would significantly improve our ability to identify the biological basis of invasiveness.

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